REPRODUCTIVE BIOLOGY OF *NYMPHAEA* (NYMPHAEACEAE)[1]

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ABSTRACT

Several reproductive strategies have evolved within the genus Nymphaea. *Sexual reproduction is mostly protogynous; flowers are open two to several days (depending on the species), with pollen release usually commencing on the second day. The five subgenera of* Nymphaea *exhibit differences in floral biology. There is considerable variation in the timing of flower opening, floral odor, flower color, and the form and function of various flower parts. These differences may contribute to genetic isolation between species both through temporal separation of flowering and attraction of different pollinators. While sexual reproduction in many species is dependent on xenogamy or geitonogamy, other species have adaptations to promote autogamy. No species of* Nymphaea *is known to be agamospermous, but several other modes of asexual reproduction are exhibited: detachable tubers, stolon formation, and proliferations of floral and foliar tissue. Wide-ranging tropical species all avoid being totally reliant on pollinators by employing one or more reproductive alternatives to outcrossing; clearly some obligate outcrossers are limited in their colonizing by pollinator availability. The most important of these reproductive alternatives is autogamy. Wide-ranging temperate species, which mostly rely exclusively on outcrossing for sexual reproduction, probably avoid pollinator limitations by utilizing a broader range of pollinators.*

Nymphaea is the largest and most widely distributed genus in the Nymphaeales. About 40 species of waterlilies, as they are commonly known, are distributed on all continents except Antarctica. The classification of Conard (1905), still generally accepted, recognizes five subgenera: the north-temperate subgenus *Nymphaea*, neotropical subg. *Hydrocallis*, and paleotropical subg. *Lotos* of the syncarpous group and the Australian subg. *Anecphya* and pantropical subg. *Brachyceras* of the apocarpous group. The success of this genus as determined by number of species and distributional range is due to several factors. Its age, dating probably from mid Tertiary (Collinson, 1980), may be one factor; however, other nymphaeoid genera of comparable age have not demonstrated the same degree of evolutionary divergence. Another factor is its specialized but widely available ecological niche. Waterlilies almost invariably inhabit still or gently flowing water over rich organic substrates. In stable aquatic habitats they root in water too deep for competing emergent vegetation. Their floating leaves, in addition, outcompete submersed leaves for light. A few other genera are competitors for this niche, including primarily nymphaeaceous genera such as *Nuphar*, *Brasenia*, and *Nelumbo*, and the distantly related genus *Nymphoides*. None of these, however, has attained the species radiation and global distribution of *Nymphaea*.

According to Gupta (1978, 1980) polyploidy, structural chromosome changes, and gene mutations have played important roles in the evolution of *Nymphaea*. The poor development of isolating mechanisms is also mentioned as being responsible for the high incidence of natural and artificial interspecific hybridization. However, such mechanisms are not altogether absent. Certainly ecological factors help isolate certain species from others, such as the alkaline-tolerant *N. tuberosa* Paine from the more acidophilic *N. odorata* Aiton, or the slightly halophilic *N. rudgeana* G. Meyer from less salt-tolerant species, or the riparian *N. potamophila* Wiersema from lacustrine species. Geographical isolation has also been a factor, such as separating *N. alba* L. of Europe from the North American *N. odorata*.

This paper, in discussing the reproductive biology of *Nymphaea*, focuses on several potential external mechanisms for reproductive isolation. Internal mechanisms (terminology from Grant, 1981) no doubt are important in promoting the hybrid breakdown and sterility often observed in *Nymphaea* (Gupta, 1978) but are outside the scope of this discussion. Differences within and among the

subgenera with regard to floral odor, flower color, the timing of floral responses, and the form and function of various flower parts may contribute to genetic isolation between species. Isolating mechanisms are probably more important for tropical and subtropical species, since their densities tend to be greater than those in temperate areas. After focusing on these potential isolating mechanisms, several adaptations relating to asexual reproduction in *Nymphaea* will be discussed, thereby permitting an evaluation of the various reproductive strategies found among waterlilies.

FLORAL BIOLOGY

Some general aspects of floral biology in *Nymphaea* should be presented. The flowers consist of 4 sepals, 7–40 petals, 20–700 stamens, and 5–47 carpels, the latter forming a ring embedded in cup-shaped receptacular and appendicular tissue to which the appendicular organs are attached laterally. The upper surface of each carpel contributes a ray of stigmatic tissue to the stigmatic disk, which tops the ovary, and this ray usually terminates abaxially in a free appendage termed the carpellary appendage or carpellary style.

Sexual reproduction is mostly protogynous. First-day flowers generally open slightly less than on later days, with the stamens and carpellary appendages, if present, spreading to permit insect visitors access to the stigmatic region. The tips of the stamens form a circular wall or palisade around a central pool of stigmatic fluid. Although variable in quantity, I have observed this fluid in all species thus far examined. It reportedly contains a surfactant primarily responsible for washing pollen from the bodies of insect visitors, but also possibly contributing to their frequently observed drownings. In second-day flowers the sepals, petals, and most of the stamens reflex fully. Anther dehiscence occurs in second-day flowers, with the stigmatic fluid drying up at or by this time. Insects are generally free to forage for pollen due to the dryer nature of the stigma and the incurving of the inner stamens and carpellary appendages over the stigmatic region. Pollen-covered insects that subsequently visit first-day flowers effect pollination. In many species first-day flowers open slightly later than on subsequent days. This ensures that insect visitors will first visit pollen-releasing flowers prior to their entrance into pollen-receptive flowers (Schneider, 1979; Meeuse & Schneider, 1980; and pers. obs.).

Floral odor. Although numerous authors have commented on the differences in floral odor among various waterlily species (Conard, 1905; Cramer et al., 1975; Prance & Anderson, 1976; Meeuse & Schneider, 1980), which range from inodorous to lightly fragrant or strongly pungent, nothing is known of the chemistry of the odor-producing compounds or their potential in attracting certain taxa of pollinators. The importance of floral odor seems to be greatest for night-blooming species, which can rely less on flower color to attract pollinators. Most members of the night-blooming subg. *Hydrocallis* emit considerable odor that is detectable for some distance. These species are probably pollinated by Coleoptera (Cramer et al., 1975; Prance & Anderson, 1976; Prance, 1980; Wiersema, 1987), in contrast to members of the day-blooming subgenera *Anecphya*, *Brachyceras*, and *Nymphaea*, which appear to be pollinated by Hymenoptera or Diptera (Van der Velde et al., 1978; Schneider & Chaney, 1981; Schneider, 1982a, b; Capperino & Schneider, 1985). The latter group has typically far less odorous flowers, with odors appearing to differ qualitatively from those of subg. *Hydrocallis*. In subg. *Anecphya*, no odor is known (Conard, 1905; Schneider, 1982b). Strong odors have not been observed in *N. lotus* L. of the night-blooming subg. *Lotos*, although nothing is known regarding insect pollinators in this subgenus.

Schneider (1982a) has hypothesized that in subg. *Hydrocallis* the highly developed carpellary appendages may help volatilize odors. A darkening of these appendages and sometimes the staminal bases is frequently observed as flowering progresses, suggesting that chemical activity may be taking place. Olfactory tests with *N. jamesoniana* Planchon support this, but additional tests are needed. In the inodorous subg. *Anecphya*, carpellary appendages are absent.

Flower color. Considerable variation in petal coloration is evident among waterlily species. Flower color is, however, relatively constant among night-blooming species, with all species of subgenera *Hydrocallis* and *Lotos* having white or nearly white petals. An exception to this trend is found in the red-flowered *N. rubra* Roxb. ex Andrews, but recent evidence suggests that this is an apomictic "species" that may not undergo sexual reproduction (Mitra & Subramanyam, 1982). Certain species of the other syncarpous subgenus, the diurnally flowering subg. *Nymphaea*, have also yielded pink- to red-flowered forms under rare circumstances (Conard, 1905; Elkins, 1970; Erixon, 1980), white being the usual petal color in all species involved. However, *N. mexicana* Zucc. of this subgenus has yellow petals. The neotropical

members of subg. *Brachyceras* are also primarily white-petaled (pale blue fading to white in *N. elegans* Hook.); those of the paleotropics are predominantly blue-petaled, although both white- and yellow-petaled species are known (Conard, 1905; Mendonça, 1960; Hutchinson & Dalziel, 1966).

Little evidence exists to evaluate the importance of flower color in *Nymphaea* in attracting different pollinators. The presence of blue and yellow color forms may be an adaptation favoring pollination by hymenopterans or dipterans, which pollinate similarly colored flowers in other plant groups (Proctor & Yeo, 1972). Schneider and colleagues have examined pollinators of the white-flowered *N. odorata* (Schneider & Chaney, 1981), the blue-flowered *N. elegans* (Schneider, 1982a), and the yellow-flowered *N. mexicana* (Capperino & Schneider, 1985). Insect visitors to all of these diurnally flowering species included Hymenoptera, Diptera, and Coleoptera, indicating that the same classes of pollinators appear to be attracted to all three flower colors. As all of these observations have come from Texas, more observations on pollinators throughout the ranges of these species, especially in situations where they coexist, are needed in order to evaluate better the importance of flower color as a factor in reproductive isolation. Valuable observations toward a resolution of this question could be made in south-central Africa where all three color forms occur.

Temporal responses. Timing of floral responses may be important in determining which pollinators are associated with a particular species, insofar as activity levels of potential pollinators may vary throughout the day or night. Species that utilize the same pollinators could still be reproductively isolated through temporal separation of flowering, which seems to provide a partial if not total barrier to gene flow between certain species. For day-blooming North American species of subg. *Nymphaea* (Fig. 1A), flowers of the widespread *N. odorata* open just after dawn and close around noon or shortly thereafter (Conard, 1905, Pennsylvania; Schneider & Chaney, 1981, Texas; Wiersema & Haynes, 1983, Alabama). In the northern portion of its range its distribution overlaps that of *N. tetragona* Georgi, whose flowers are open from just before noon to around 5:00 P.M. (Conard, 1905, cultivation in Pennsylvania). The sequence of floral opening proceeds from the sepals and outer petals gradually inward to the inner stamens and requires ½–1 hour, as does floral closure. First-day flowers (pollen-receptive) generally open slightly later than those of subsequent days. The important times to consider are the periods when the stigmas of first-day flowers are accessible to potential pollen donors and the stamens of later flowers accessible to potential pollen acceptors. Allowing for the adjustments just mentioned, it is probable that complete temporal separation exists between *N. odorata* and *N. tetragona*, although field data are needed from areas of sympatry to support this assumption. Similarly, *N. mexicana*, whose flowers open ca. 11:00 A.M. and close ca. 4:00 P.M. (Conard, 1905, cultivation in Pennsylvania; Wiersema & Haynes, 1983, Alabama; Capperino & Schneider, 1985, Texas), achieves some degree of temporal separation from *N. odorata*, with which it is sympatric over parts of the southeastern United States. Less than an hour overlap appears to be present in the flowering schedules of these two species, which have different-colored flowers, and occasional natural hybrids occur (Ward, 1977, Florida and Georgia; Wiersema & Haynes, 1983, Alabama). On the other hand, the flowering schedules of *N. odorata* and the closely related *N. tuberosa* (Conard, 1905, Pennsylvania) overlap considerably (3–4 hours), and not surprisingly, their taxonomic relationship remains confused (Conard, 1917; Monson, 1960; Williams, 1970).

Available information on the day-flowering species of subg. *Brachyceras* in the New World (Conard, 1905; Prance & Anderson, 1976; Schneider, 1982a) indicates considerable overlap in the flowering schedules of the three species (Fig. 1B). Data are lacking for most Old World taxa of this subgenus.

Considerable information on flowering schedule in the nocturnally flowering, neotropical subg. *Hydrocallis* has been gathered from outdoor cultivation in Alabama (Wiersema, 1987). Cultivated samples of those species obtained from two or more regions exhibited little variation in flowering schedule. Among most species sufficient overlap in flowering time was observed to negate the importance of this feature as a barrier to genetic exchange between species (Fig. 1C). This is particularly true of species that complete flowering before midnight. Species, such as *N. amazonum* C. Martius & Zucc. and *N. prolifera* Wiersema, whose flowers remain open after midnight, are provided some degree of genetic isolation. In *N. prolifera* second-day flowers, although opening at dusk, remain mostly inaccessible to pollinators due to delayed reflexing of the inner petals and stamens until after midnight, when flowers of most other species have closed. In *N. amazonum* floral responses reach their greatest specialization. First-day flowers open fully and close during the two hours just preceding dawn. Second-day flowers open at dusk, remain open throughout
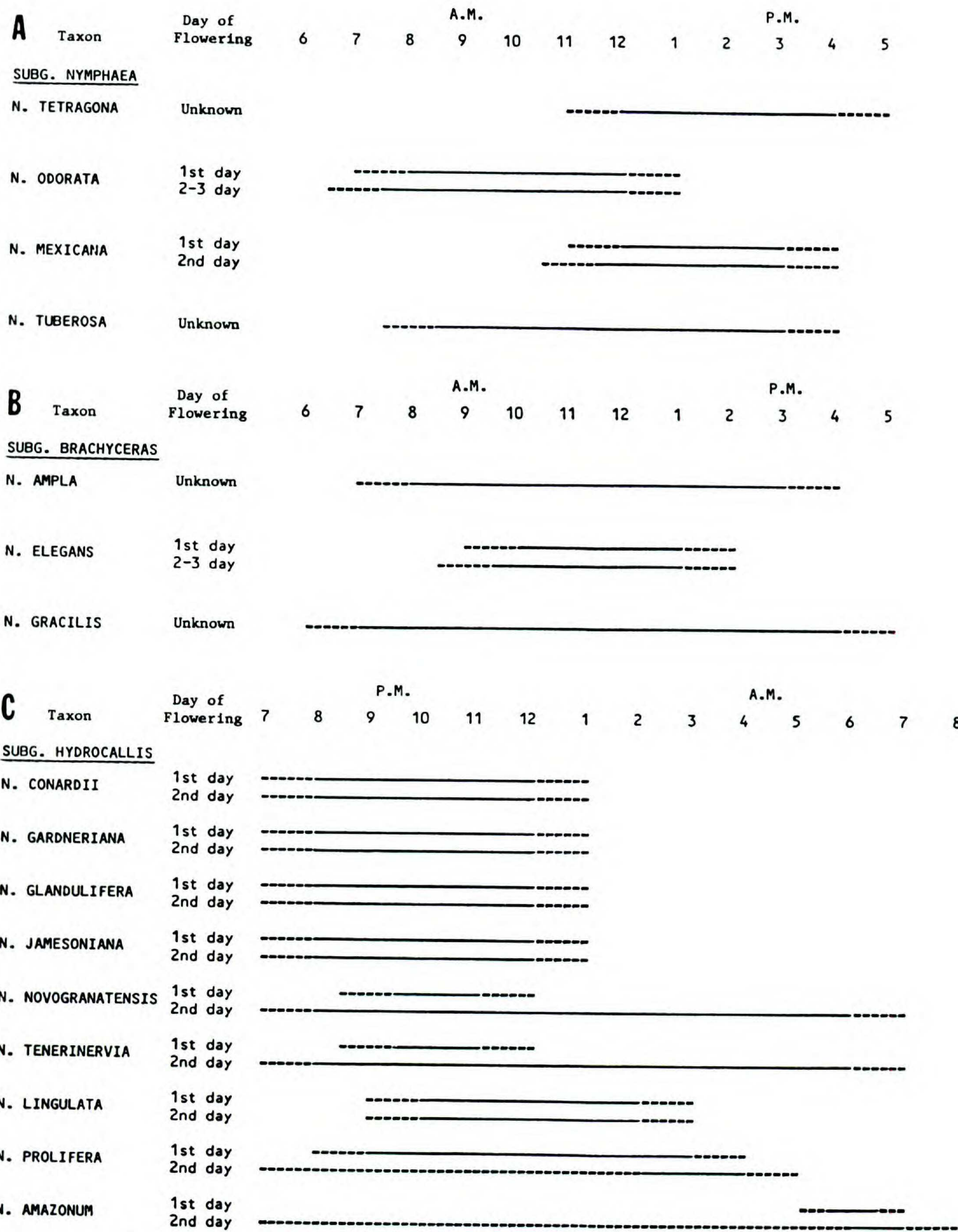
FIGURE 1. Flower-opening times for selected species of Nymphaea. Data sources indicated in text. Dashed lines = partially open flowers, solid lines = fully open flowers.—A. North American species of subg. Nymphaea.—B. Neotropical species of subg. Brachyceras.—C. Subg. Hydrocallis.

the night, and close in the early dawn. Their anthers do not dehisce until a few hours before dawn when cross-pollination[3] of first-day flowers is possible. Thus *N. amazonum* is effectively isolated reproductively from other species of subg. *Hydrocallis* even though it may make use of the same pollinators (Cramer et al., 1975).

Floral responses in the night-blooming subg. *Lotos* have received little or no attention. Flowers here reportedly open at dusk and remain open until ca. 11:00 A.M. the following morning (Conard, 1905; Hutchinson & Dalziel, 1966; Wiersema, 1982). First-day (pollen-receptive) flowers of *N. lotus* I observed in cultivation did not open for this lengthy period, but were open for only a few hours around midnight. If these observations are consistent with natural populations, for which scrutinous data are lacking, then cross-pollination in some species of this subgenus could occur only at night, with the diurnal portion of flowering on later days, providing no opportunity for successful cross-pollination.

No evidence suggests that seasonal separation of flowering periods exists in *Nymphaea*. Waterlilies usually commence flowering once sufficient vegetative growth has occurred and continue flowering throughout the growing season. In many populations of *N. prolifera* and *N. lasiophylla* C. Martius & Zucc., however, normal flowers are replaced by tuberiferous flowers (see page 801) during part or all of the growing season. This does not seem to be temporal separation of flowering but rather a shift from sexual to asexual reproduction, the former not being successful in areas where this phenomenon has been observed.

In many species the flowering cycle is extended, with anther dehiscence continuing into a third or fourth day. Species with extended flowering cycles increase the percentage of pollen-releasing (or functionally male) flowers relative to first-day (or functionally female) flowers. Thus the percentage of insect visits involving female flowers would be reduced, but larger pollen loads might be found on insects (Capperino & Schneider, 1985). A longer flowering cycle might also attract more pollinators to a population by displaying a greater number of open flowers.

Other floral modifications. A number of ad-

ditional morphological or behavioral differences in flowers have been noted among waterlilies. The functional significance of many of these has yet to be determined. Perhaps the foremost among them relates to the carpellary appendages, which are absent in subg. *Anecphya*, triangular to tapering in subgenera *Nymphaea* and *Brachyceras*, and most strongly developed in subgenera *Lotos* and *Hydrocallis*, the only night-blooming subgenera, where they are linear to highly clavate. They attain a length of nearly 3 cm in some flowers of *N. oxypetala* Planchon of subg. *Hydrocallis*. The structural differences in these appendages among species of *Nymphaea* suggest differences in function. Hypotheses concerning the function of the carpellary appendages have suggested that they may serve as a source of food, a source of heat, or a source of volatile odor-producing compounds (Meeuse & Schneider, 1980; Prance, 1980; Schneider, 1982a, b). Similar structures in the related genus *Victoria* Lindley, which exhibits a night-blooming beetle-pollination syndrome, are known to have both thermogenic and nutritive functions (Knoch, 1899; Valla & Cirino, 1972; Prance & Arias, 1975). An additional function of undetermined importance for such appendages in *Nymphaea* may be to control access to the stigmatic disk. In first-day flowers the appendages are erect or spreading, allowing free access to the stigmatic region; however, in second-day and later flowers they are incurved over the stigma. In species such as *N. lotus* of subg. *Lotos* or *N. amazonum* of subg. *Hydrocallis*, they completely cover the stigma. In many species, especially diurnal species with less-developed appendages, the inner stamens form part of this barrier.

It has been suggested that the carpellary appendages may play a role in deepening or broadening the pool of stigmatic fluid and thus improving the ability of flowers to wash pollen from the bodies of insect visitors. However, *N. gigantea* Hook. of subg. *Anecphya*, which lacks carpellary appendages, does not appear to exhibit any reduction in the size of the stigmatic pool (Schneider, 1982b). Comparisons of the quantity of stigmatic fluid among *N. elegans*, *N. odorata*, and *N. mexicana* by Capperino & Schneider (1985) contradict this hypothesis as well, as flowers of *N. elegans*, with the least-developed appendages, produce the greatest amount of fluid.

In the pantropical, diurnally flowering subg. *Brachyceras*, the stamens bear prolonged connective appendages in many species. These appear to form the inner surface of an oil-covered and very

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[3] As some species of *Nymphaea*, including *N. amazonum*, are clonal, cross-pollination as here used may involve either xenogamy or geitonogamy, in contrast to self-pollination involving autogamy.

slippery circular palisade surrounding the central pool of stigmatic fluid in first-day flowers. Insect visitors that enter this region inevitably fall into the stigmatic pool where pollen is washed from them. The same result is achieved in the diurnally flowering subg. *Anecphya* by means of the large number of weakly supported, nodding stamens having narrow filaments, which form an almost insurmountable wall around the stigmatic region (Schmucker, 1932; Meeuse & Schneider, 1980).

Flowers of certain species of *Nymphaea* are characterized by abundant sclereids in some floral parts. In *N. caerulea* Savigny of subg. *Brachyceras*, elongate bipolar or acicular sclereids are found in the stamens (Chifflot, 1902). In several species of subg. *Hydrocallis*, such acicular sclereids are abundant throughout the staminal tissue, and in a few species they are evident in the stigmatic ray tissue as well. In *N. oxypetala* of this subgenus, tiny spherical sclereids are produced in and apparently released from staminal tissue adjacent to the anther sacs (Chifflot, 1902; Wiersema, 1987). Asterosclereids and trichosclereids are also found in the floral tissues of certain species (Malaviya, 1962). All of the sclereids mentioned above are impregnated with calcium oxalate crystals. It has been suggested that the asterosclereids or trichosclereids may provide support (Conard, 1905; Malaviya, 1962) or internal water recovery (Schanderl, 1973). Neither of these explanations is sufficient to explain the spherical sclereids found in stamens of *N. oxypetala* or perhaps the great abundance of acicular sclereids in stamens in other members of subg. *Hydrocallis*. That these structures may help deter beetle predation on floral parts has not been investigated.

Differences in pollen morphology exist within *Nymphaea*. The pollen of night-blooming and presumably beetle-pollinated subgenera is smoother than the highly puckered or ornamented pollen of the three diurnally flowering subgenera, which are apparently pollinated by bees and/or flies (Wiersema, 1987).

Waterlily seeds also vary. Those of temperate members of subg. *Nymphaea* are completely devoid of surface papillae, whereas those of tropical subgenera usually bear numerous surface papillae in various arrangements. A basic difference between the environmental requirements of temperate vs. tropical seeds is that the former must be adapted to endure colder (and perhaps freezing) temperatures, whereas the latter must often withstand periods of drought. Indeed, seeds of most temperate species exhibit little resistance to drought (Conard, 1905), and those of many tropical species

do not tolerate freezing. It is hypothesized that the surface papillae may be important in conferring drought resistance to tropical seeds, perhaps by absorbing water. It is interesting to note that *N. mexicana*, a subtropical member of the mostly temperate subgenus *Nymphaea*, has papillose seeds.

A number of waterlily species produce seeds without cross-pollination. In those thus far examined, autogamy rather than agamospermy has been responsible (Wiersema, 1987). Two different methods are employed in producing seeds autogamously. One involves homogamy, the early dehiscence of stamens on the first day of flowering when the stigma is receptive to pollen. I have observed this in *N. jamesoniana* and *N. lingulata* Wiersema of subg. *Hydrocallis* and *N. ampla* (Salisb.) DC. of subg. *Brachyceras*, and it has been reported for *N. alba* of subg. *Nymphaea* (Heslop-Harrison, 1955). The second method involves maintaining the receptivity of the stigma in second-day flowers, such that pollen being released at the normal time can effect self-pollination. This method is apparent in several taxa of subg. *Hydrocallis*, such as *N. amazonum* subsp. *amazonum*, *N. conardii* Wiersema, and *N. rudgeana*. Autogamy has also been reported among other members of subg. *Brachyceras*, such as *N. caerulea* and *N. stellata* Willd. (Conard, 1905). In the latter species and in *N. ampla* (Prance & Anderson, 1976), reports have suggested pollen release in buds.

With the exception of the reports concerning autogamy in the temperate day-flowering *N. alba*, all other reports of autogamy involve tropical diurnally and nocturnally flowering species. No records of autogamy are known for subgenera *Lotos* or *Anecphya*.

ASEXUAL REPRODUCTION

A number of asexual modes of reproduction are employed by waterlily species. The most widespread is stolon formation, as in *N. lotus* of subg. *Lotos*; *N. amazonum*, *N. gardneriana* Planchon, *N. lasiophylla*, *N. lingulata*, and *N. tenerinervia* Caspary of subg. *Hydrocallis*; and *N. mexicana* of subg. *Nymphaea*. In *N. mexicana*, stolons are of greater diameter and develop an unusual terminal perennating structure at the end of the growing season. This structure consists of a compact series of leaf buds from which hang several starch-laden roots reminiscent of a bunch of bananas, hence the common name "banana waterlily."

Several other members of subgenus *Nymphaea*, namely *N. odorata*, *N. tuberosa*, *N. alba*, and *N. candida* J. S. Presl, possess horizontal rhizomes in

contrast to the erect rhizomes of all other species. Several shoots may eventually develop from a single horizontal rhizome. On the main rhizome of *N. tuberosa* small tuberous shoots develop which, due to a constricted area at their base, are readily detachable and serve as propagules.

Two other forms of asexual reproduction have been observed, one involving proliferation of floral tissues, the other proliferation of leaf tissues. In the former, all but the outermost appendages of flowers are aborted, and an enlarged tuber is formed centrally which gives rise to whorls of leaves and additional tuberiferous flowers. A few orders of branching may result, leading to the formation of a large number of small tubers. The tubers readily abscise, float briefly, and eventually become rooted and develop into mature plants. This process occurs regularly in the neotropical *N. lasiophylla* and *N. prolifera* of subg. *Hydrocallis* (Wiersema, 1987). Similar abortive flowers have been reported in other syncarpous *Nymphaea* (Bose, 1961; Mohan Ram & Nayyar, 1974; Majeed Kak, 1977; Mitra & Subramanyam, 1982) but only as an unusual occurrence. This is a very effective method of reproduction and dispersal, particularly in *N. prolifera*, which commonly inhabits lowland savannas subject to periodic flooding.

Proliferation of leaf tissue occurs in *N. micrantha* Guillemin & Perrottet of subg. *Brachyceras*. In this species new plants are formed on the upper surface of a leaf opposite the insertion of the petiole. These develop extensively only after the leaf is detached from the parent plant (Conard, 1905; Hutchinson & Dalziel, 1966). The effectiveness of this reproductive process is unknown. *Nymphaea micrantha* is found only in west tropical Africa.

Evaluation of Reproductive Strategies

Perhaps the best way of evaluating the overall reproductive strategies of waterlilies is to examine distributional ranges of various species as reflections of their colonizing abilities. Reproductive strategy is one of several factors that contribute to distributional success. Table 1 provides a ranking of temperate, subtropical, and tropical species derived from their natural ranges. Such a measure cannot account for differences in population frequency within ranges, hidden instances of artificial dispersal, or problems of questionable taxonomy; however, it is still useful. Table 1 also provides information on the reproductive alternatives employed by each species, insofar as information is available. All of these species are assumed to be capable of normal sexual outcrossing. Several ques-

tionable species from the paleotropics have been excluded.

Two elements seem to be important in interpreting the colonizing ability of a given species, its dispersal capability, and its ability to become established and persist in a new location. In cases involving overland dispersal, seeds are the probable dispersal units and waterbirds the likely agents. Although most aspects of seed release appear to be similar among the various species, the number of seeds per fruit and the size of the seeds are two variables that could affect dispersal capability. *Nymphaea tetragona*, which is dispersed solely by seeds, has comparatively large seeds with relatively few per fruit, two traits that could potentially retard dispersal. However, *N. tetragona* has the broadest distribution of any species. Even *N. mexicana*, having the largest seeds (almost twice as large) with the fewest per fruit of any *Nymphaea* species, has been successfully dispersed along the Gulf Coast of North America. The smallest and probably most numerous seeds are found in *N. jamesoniana*, the most widely distributed neotropical species. Thus there appears to be little relationship between these seed variables and dispersal capability, which appears to be adequate for most species.

If dispersal factors do not appear to limit overall distribution, then factors relating to establishment must be considered more important. Ecological factors certainly affect germination, seedling development, and successful maturation of a colonizing species. If these initial barriers can be overcome, establishment and long-term survival in a new environment become heavily dependent on reproductive ability.

Several key observations can now be made with reference to Table 1. All ten of the most widely distributed tropical species utilize at least one reproductive alternative to total reliance on xenogamy or geitonogamy. In seven of the ten this alternative is autogamy. Of the ten most narrowly distributed species, only one is known to be autogamous. As already mentioned, reproductive strategy is one of several factors that affect overall species distributions. However, in terms of distributional success for tropical *Nymphaea* species, autogamy seems to be the most important reproductive alternative.

The importance of autogamy to tropical waterlily species is to provide for seed production in the absence of potential pollinators and to enhance seed production when xenogamy or geitonogamy become inefficient. It also would eliminate the need for a second individual in colonizing situations; however, this obstacle is easily overcome by clonal or

TABLE 1. *Distributional success of* Nymphaea *species in relation to reproductive strategy. All species known or assumed to be capable of xenogamy. Data mostly from Conard (1905), Wiersema (1987), or personal observation.*

Species	Subgenus	Index[1]	Reproductive alternatives[2]	
			Autogamy	Asexual
TEMPERATE				
N. tetragona	Nymphaea	310		
N. candida	Nymphaea	130		HR
N. alba	Nymphaea	110	A	HR
N. odorata	Nymphaea	90		HR
N. tuberosa	Nymphaea	30		HR
SUBTROPICAL				
N. elegans	Brachyceras	40		
N. mexicana	Nymphaea	35		S
TROPICAL				
N. lotus	Lotos	140		S
N. jamesoniana	Hydrocallis	125	A	
N. ampla	Brachyceras	115	A	
N. caerulea	Brachyceras	115	A	
N. amazonum	Hydrocallis	100	A	S
N. rudgeana	Hydrocallis	100	A	
N. conardii	Hydrocallis	90	A	
N. nouchalii	Lotos	90		S?
N. prolifera	Hydrocallis	90		FLP
N. stellata	Brachyceras	85	A	
N. capensis	Brachyceras	70		
N. gardneriana	Hydrocallis	70		S
N. oxypetala	Hydrocallis	70		
N. glandulifera	Hydrocallis	65	A	
N. gigantea	Anecphya	60		
N. tenerinervia	Hydrocallis	40		S
N. lingulata	Hydrocallis	35	A	S
N. lasiophylla	Hydrocallis	30		FLP, S
N. micrantha	Brachyceras	30		FOP
N. gracilis	Brachyceras	20		
N. petersiana	Brachyceras	20		
N. potamophila	Hydrocallis	20		
N. sulphurea	Brachyceras	20		
N. novogranatensis	Hydrocallis	15		

[1] Latitudinal range + longitudinal range (in degrees).
[2] HR = horizontal rhizomes; S = stolons; FLP = floral proliferation; FOP = foliar proliferation.

multiple-flowered individuals, as there is no evidence of self-incompatibility in *Nymphaea*. In the neotropics several night-blooming species of subg. *Hydrocallis*, such as *N. prolifera*, *N. gardneriana*, *N. lasiophylla*, and *N. tenerinervia*, rarely produce seeds in natural populations, although they are capable of seed production if cross-pollinated (Wiersema, 1987). Reports on pollinators in this subgenus have implicated only scarab beetles of the genus *Cyclocephala* Latreille (Cramer et al., 1975; Prance & Anderson, 1976; Prance, 1980; Wiersema, 1987). Asexual reproduction has seem-

ingly allowed the four species mentioned to exist in areas where these pollinators are absent. Further overland expansion from such sites is probably more difficult in the absence of seed production. Nonautogamous species without asexual alternatives would be completely restricted by pollinator availability. The narrow distribution of most tropical species in this latter category suggests that pollinator distribution may be an important element in restricting their spread.

The paleotropical and widespread *N. lotus* and *N. nouchalii* Burm. f. of the night-blooming subg.

Lotos have not been observed to be autogamous, however. To account for the distributional success of these taxa either: a) autogamy has gone undetected, b) the pollinators utilized are more widely distributed or a range of pollinators is used, or c) stolons are more effectively employed in dispersal than in other waterlily species. A fourth possibility, that of human dispersal, may account for some of this distribution, as these species are cultivated, and the existence of *N. lotus* in the neotropics has been attributed to artificial introduction (Wiersema, 1982). However, floristic accounts have considered them indigenous throughout most of their paleotropical ranges.

In temperate species, all of subg. *Nymphaea*, autogamy is clearly not as important in conferring distributional success, as it has been observed only in one species. With the exception of the detachable tubers produced by *N. tuberosa*, seeds are the only effective dispersal agent produced in this subgenus. How then are the limits of pollinator availability overcome by wide-ranging temperate species? These diurnally flowering species either employ pollinators that are more widely distributed or utilize a range of pollinators. The latter explanation is probably correct, in view of the variety of insect visitors reported for day-blooming species in temperate regions (Robertson, 1889; Conard, 1905; Meeuse & Schneider, 1980; Schneider & Chaney, 1981; Schneider, 1982a; Capperino & Schneider, 1985), but it needs to be confirmed with comprehensive studies of species–pollinator relationships.

Pollinator relationships of most tropical day-blooming species in subgenera *Anecphya* and *Brachyceras* remain to be assessed; however, in subg. *Brachyceras* autogamy has become an important alternative to total reliance on outcrossing.

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